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Distribution of terrestrial Enchytraeidae in Ireland[1])

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With 9 figures

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1. Introduction

The Irish Enchytraeidae are now fairly well known and eighty-one species are recorded (SOUTHERN 1909, 1913; HEALY 1975, 1976, 1978). The fauna of terrestrial habitats appears to be rich, especially in the wet soils which are characteristic of the country. A survey carried out in 1972–1974 had a dual purpose: (1) to compile a species list for the country and record the distribution of species according to recognised vegetation types and (2) by analysing the soils from the different sites, to determine the preferred levels and limits of tolerance for the different species in relation to various physical and chemical parameters. The results of this survey, together with details of sampling and analytical procedures and descriptions of sampling sites are given in HEALY (1976). This paper summarises the more important findings concerning ecological limits and preferences.

An animal's ability to live and reproduce in a given place is determined by its capacity to tolerate the complete range of environmental conditions it will encounter and its competitive powers vis-à-vis other members of the community both within its own trophic level and at higher levels. The determination of tolerance ranges in the field is difficult, however, because of spatial and temporal variation in environmental levels and because the various factors interact to affect each other as well as the responses of the organism. Indeed, some ecologists consider any analysis of individual factors to be meaningless. However, a knowledge of the apparent factors which limit species distribution, even if these are not fully understood, has practical uses and both ecologists and taxonomists rely on such information to describe the distributional characteristics of species.

Little is known about the ecology of most enchytraeid species. It was decided therefore that despite the difficulties involved in sampling and interpretation of results, an attempt should be made to discover the way in which species distribution is influenced by soil factors. In this investigation, the ecological limits and preferences of some common Irish enchytraeids are deduced from the results of quantitative sampling using two criteria: frequency of occurrence and the presence of high density populations.

2. Methods

Since the ecological limits of a species will only be detected if sampling is carried out at and beyond these limits, a sampling programme was designed to cover as complete a range as possible of conditions, including environmental extremes, e.g. wet, dry, acid, base-rich and salty soils. Particular attention has been paid to ecotones and intermediate type habitats which are frequently ignored in ecological work. Altogether, 178 non-marine sites were selected representing the following vegetation types: bog (16 sites), flush (9 sites), wet heath (13 sites), acid grassland (19 sites), neutral grassland (17 sites), marsh (22 sites), fen (9 sites), aquatic habitats (13 sites), coniferous woods (8 sites), deciduous woods (24 sites), coastal sand dunes and sea-cliffs (28 sites).

[1]) Contribution to the International Symposium on Oligochaeta (Padova, 07.–10. 09. 1977).

In view of the time required to analyse quantitative samples (in most cases each individual must be examined microscopically while alive), only two sample cores, 6.2 cm diameter and 5 cm depth, were taken at each site — 356 samples in all. Such sampling is obviously inadequate if an estimation of population densities at each site is required but this was not the intention. In the analysis of results which follows, the whole of the sampling area (approximately 40,000 km^2) is considered as one vast sampling locality in which the pairs of sample units lie on a continuum of environmental gradients. To avoid some of the more extreme seasonal differences, sampling was confined to the period October to May.

Enchytraeids were extracted from samples using the wet-funnel method (O'Connor 1955). Environmental measurements were made on soil taken from immediatedly beside the cores. Water content (measured as % of the wet weight), *p*H and organic content (as loss on ignition) were measured for all samples. Analyses of organic carbon, total nitrogen, exchangeable calcium, potassium, phosphorus, magnesium and sodium were done on single, bulked samples for each site.

3. Results

3.1. Distribution in ecological different sites

Frequency of occurrence and density of 30 common species were correlated with 12 environmental factors: vegetation, soil texture, water content, organic content, total nitrogen, C/N ratio, *p*H and exchangeable calcium, potassium, phosphorus, magnesium and sodium. The species are listed in Table 1 together with the number of sites in which they occur and maximum and mean densities.

Most authors when recording the habitat of terrestrial organisms refer to the dominant plants, e.g. "beech wood", "grassland", "*Juncus* marsh". It is important to note therefore that most enchytraeid species were found in a wide range of plant associations. Among the 30 species considered here, 24 occurred in at least 6 of the 11 vegetation types and several

Table 1. Frequency and abundance of 30 species arranged in order of frequency

	No. of samples	Max. No. per sample	Mean No. per sample	± SE	Mean No. per m^2
Enchytraeus buchholzi Vejd.	132	91	11.4	1.4	3,808
Cognettia sphagnetorum (Vejd.)	113	250	60.4	5.6	20,000
Marionina argentea (Michaels.)	105	208	19.0	2.9	6,346
Achaeta bohemica (Vejd.)	99	158	19.0	2.5	6,346
Buchholzia fallax Michaels.	96	175	16.5	2.9	5,511
Cernosvitoviella atrata (Bretsch.)	86	184	24.2	4.4	8,082
Henlea perpusilla Friend	63	144	12.9	3.1	4,309
Marionina clavata N. et C.	62	724	52.5	13.6	17,535
Cognettia glandulosa (Michaels.)	59	185	18.6	4.5	6,212
Fridericia perrieri (Vejd.)	59	44	7.9	1.1	2,505
Achaeta affinis N. et C.	58	269	22.5	5.6	7,520
Enchytronia parva N. et C.	56	49	11.4	1.7	3,808
Fridericia galba Hoffm.	55	22	4.5	0.6	1,503
Fridericia bulboides N. et C.	46	56	7.2	1.5	2,405
Cognettia hibernica Healy	43	44	9.4	1.5	3,140
Fridericia aurita Issel	35	49	8.7	1.9	2,906
Marionina communis N. et C.	32	34	5.9	1.4	1,971
Fridericia paroniana Issel	29	19	5.3	0.8	1,170
Fridericia bulbosa (Rosa)	29	52	5.8	1.9	1,937
Mesenchytraeus sanguineus N. et C.	28	73	8.5	2.7	2,839
Cognettia cognettii (Issel)	28	60	10.9	2.6	3,641
Mesenchytraeus armatus Levins.	28	23	5.7	1.2	1,904
Henlea ventriculosa Udekem.	25	26	4.7	1.1	1,570
Cernosvitoviella sphaerotheca Healy	25	95	14.0	5.1	4,676
Fridericia bisetosa Levins.	22	35	5.1	1.0	1,703
Fridericia hegemon (Vejd.)	19	4	1.4	0.1	467
Achaeta aberrans Niet C.	19	25	7.4	1.4	2,472
Fridericia sylvatica Healy	17	36	6.2	2.0	2,071
Marionina riparia Bretsch.	15	232	28.0	15.5	9,340
Fridericia connata Bretsch.	12	33	8.2	2.9	2,739

Total number of samples = 356.

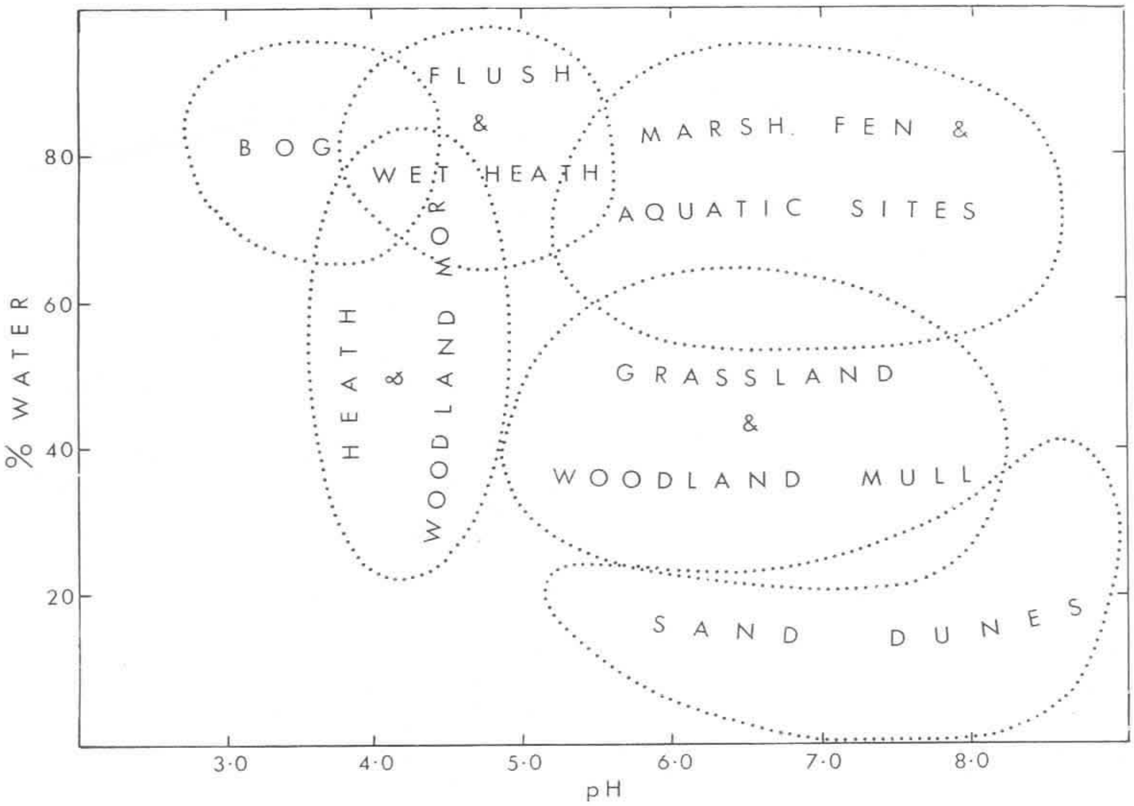


Fig. 1. Relationship between pH and water content in the different vegetation types.

reached high densities in two or more quite different types, e.g. *Marionina clavata* and *Achaeta affinis* in bogs and coniferous woods or *Fridericia perrieri* in heath and marsh. The nature of the vegetation cover is not important therefore except insofar as it determines soil properties. The most important physical characteristic of soil appears to be the proportion of humus. Many species were confined to, or showed a distinct preference for organic soils and none of the common species was absent from organic soils.

Among other edaphic factors, the closest relationships between enchytraeids and environmental levels were found for water content and pH; these results are therefore discussed in some detail. The vegetation types corresponding to the various pH and water levels are shown in Figure 1. Some of the more interesting effects of other factors are discussed briefly.

Enchytraeids have been found in soils ranging from submerged river beds to mobile sand dunes with as little as 1% water. A frequency histogram for water content (Figure 2a) shows two peaks, one in the 30—40% class, representing the usual level for most grassland and deciduous woods in the autumn-spring period, the other in the 80—90% class which contains most of the heath and marsh sites. Samples with 50—60% water are relatively rare and are mainly from woodland. Only 24 samples, mostly from sand dunes, have a moisture content less than 20%. The mean number of enchytraeids per sample (Figure 2b) increases with moisture to reach a maximum of 157 in the 60—70% range. A water content greater than 80% apparently depresses enchytraeid numbers. The number of species per sample (Figure 2c) is low in both very wet and very dry soils for which few species are well adapted and highest in the middle range where both "wet" and "dry" species may be found together.

The pH range for the samples is 2.9—8.9. The frequency histogram for 11 pH classes (Figure 3a) is bimodal with a peak at 4.0—4.5 representing heaths and coniferous woods and another at 7.0—7.5, the usual reaction of eutrophic soils e.g. lowland grassland, marsh and deciduous woods. The few samples in the 5.5—6.0 range are mainly from flushes in bog and heath which form a small proportion of the habitats sampled. The mean number of enchytraeids per sample is highest at 3.5—4.0 and falls with increasing pH to reach its lowest level above 7.5 (Figure 3b). The mean number of species per sample is only 2.8 in soils with a pH less than 3.5 and reaches a maximum of 12.5 at 6.5—7.0, falling again above this level (Figure 3c).

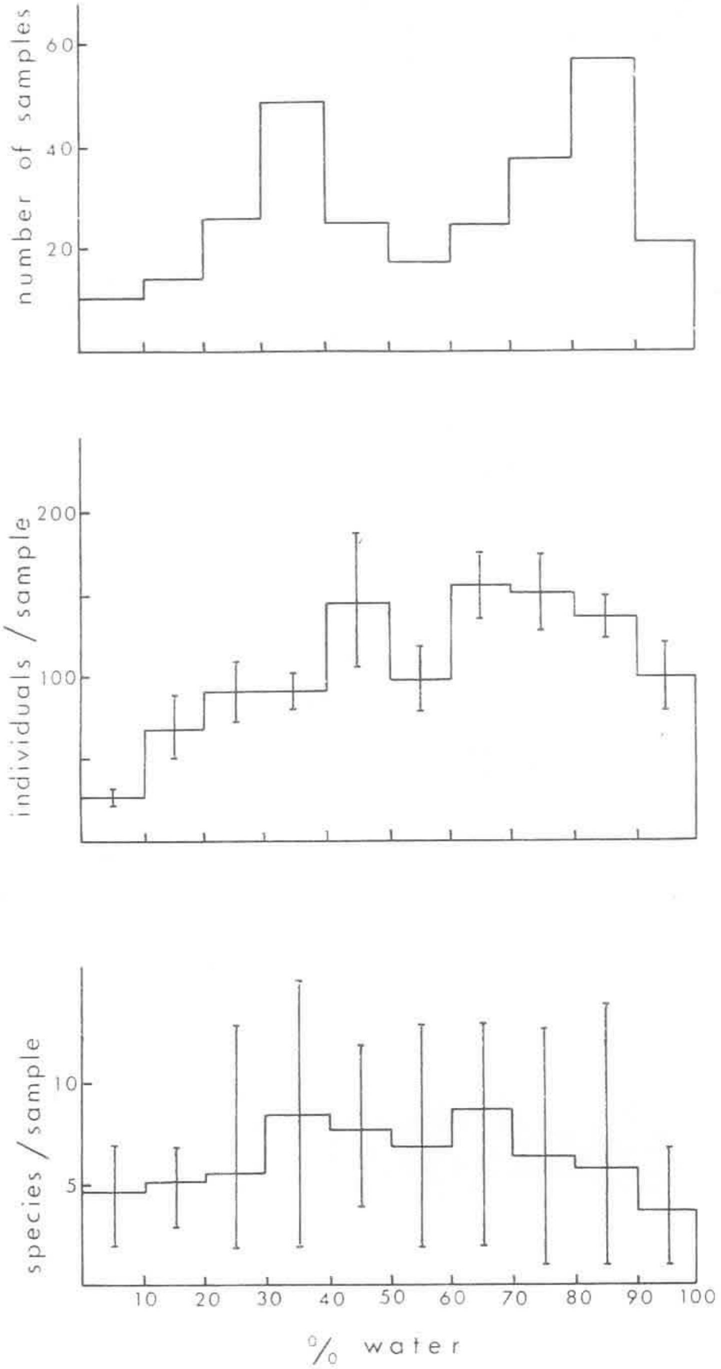


Fig. 2. Enchytraeid abundance and diversity in relation to water content. (a) Number of samples, (b) mean number of individuals per sample ± S.E. and (c) mean number of species per sample and range.

3.2. Frequency of occurrence in relation to water content

The frequency of occurrence of 30 species is expressed as a percentage of samples in each water content class in which the species occurs (Figure 4). It is seen that only *Enchytraeus buchholzi* is found at all moisture levels. Some species are absent from high, others from low water levels and several have quite a narrow range. Five groups of species may be distinguished:

(1) Most frequent in very wet soil > 80% water: *Mesenchytraeus sanguineus*, *Achaeta aberrans*, *Marionina riparia*, *Cernosvitoviella sphaerotheca*, *C. atrata*, *Cognettia sphagnetorum*.

(2) Most frequent in wet soils 70–80% water: *Cognettia glandulosa*, *C. hibernica*, *Mesenchytraeus armatus*, *Fridericia perrieri*, *Marionina clavata*.

(3) Most frequent in moist soils 50–70% water: *Cognettia cognettii*, *Achaeta affinis*, *Henlea perpusilla*, *Marionina argentea*, *Fridericia aurita*, *F. sylvatica*.

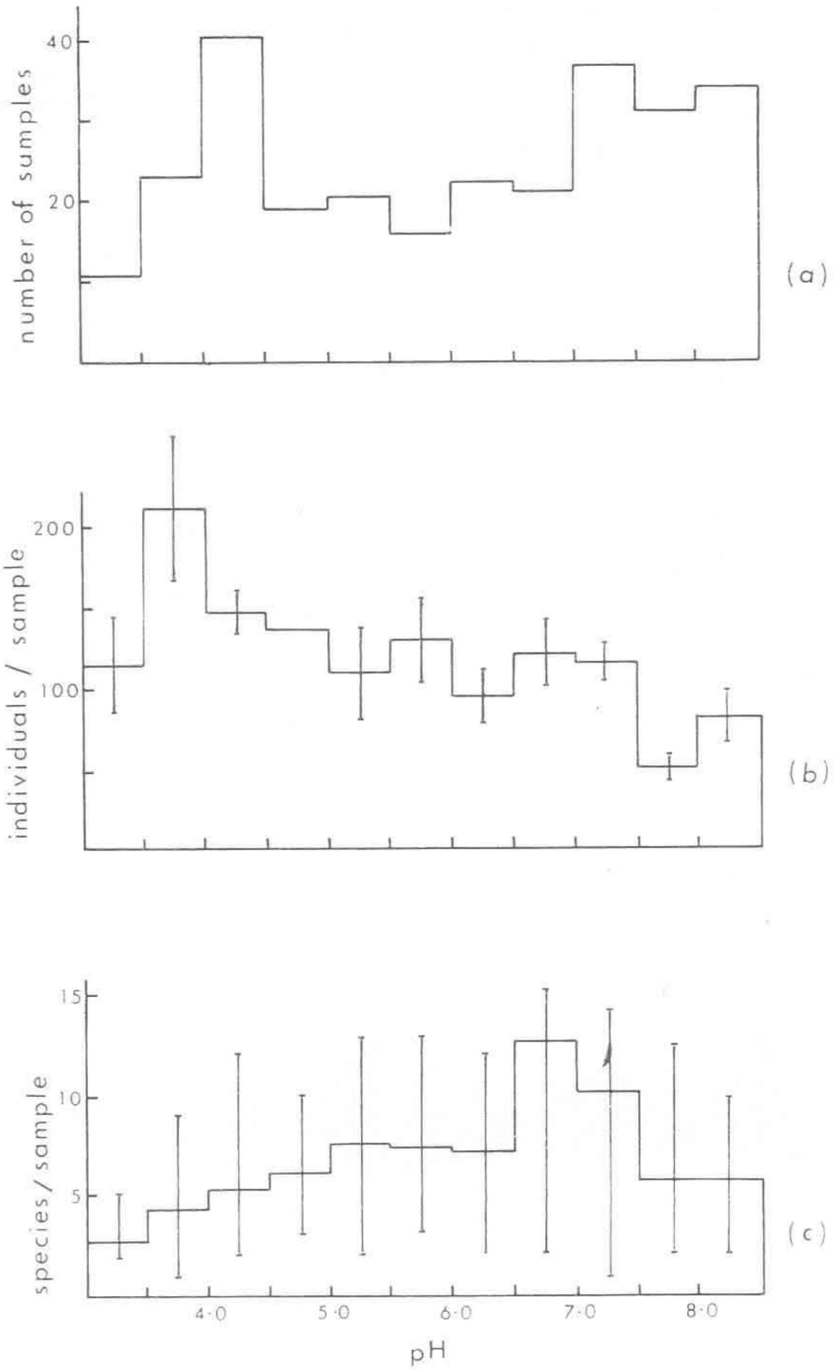


Fig. 3. Enchytraeid abundance and diversity in relation to soil *p*H. (a) Number of samples, (b) mean number of individuals per sample ± S.E. and (c) mean number of species per sample and range.

(4) Most frequent in moderately dry soils — 30–50% water: *Achaeta bohemica, Enchytronia parva, F. galba, F. bisetosa, F. connata, F. hegemon, F. paroniana, Marionina communis.*

(5) Species frequent in dry soils — < 20% water: *Buchholzia fallax, Enchytraeus buchholzi, Fridericia bulbosa, Henlea ventriculosa.*

Only a small number of samples fall into this category (Figure 2a), peaks may therefore be due to sampling error. All four species show other peaks in the middle range. In the case of *B. fallax*, it is believed that two varieties are involved (HEALY 1976).

The amount of water present in a soil depends to some extent on the quantity of organic matter which, as already mentioned, appears to be important for some species. The frequency histograms for organic matter do, in fact, show the same trends as for water but more are polymodal and the distribution is generally wider so that correlation appears to be less close.

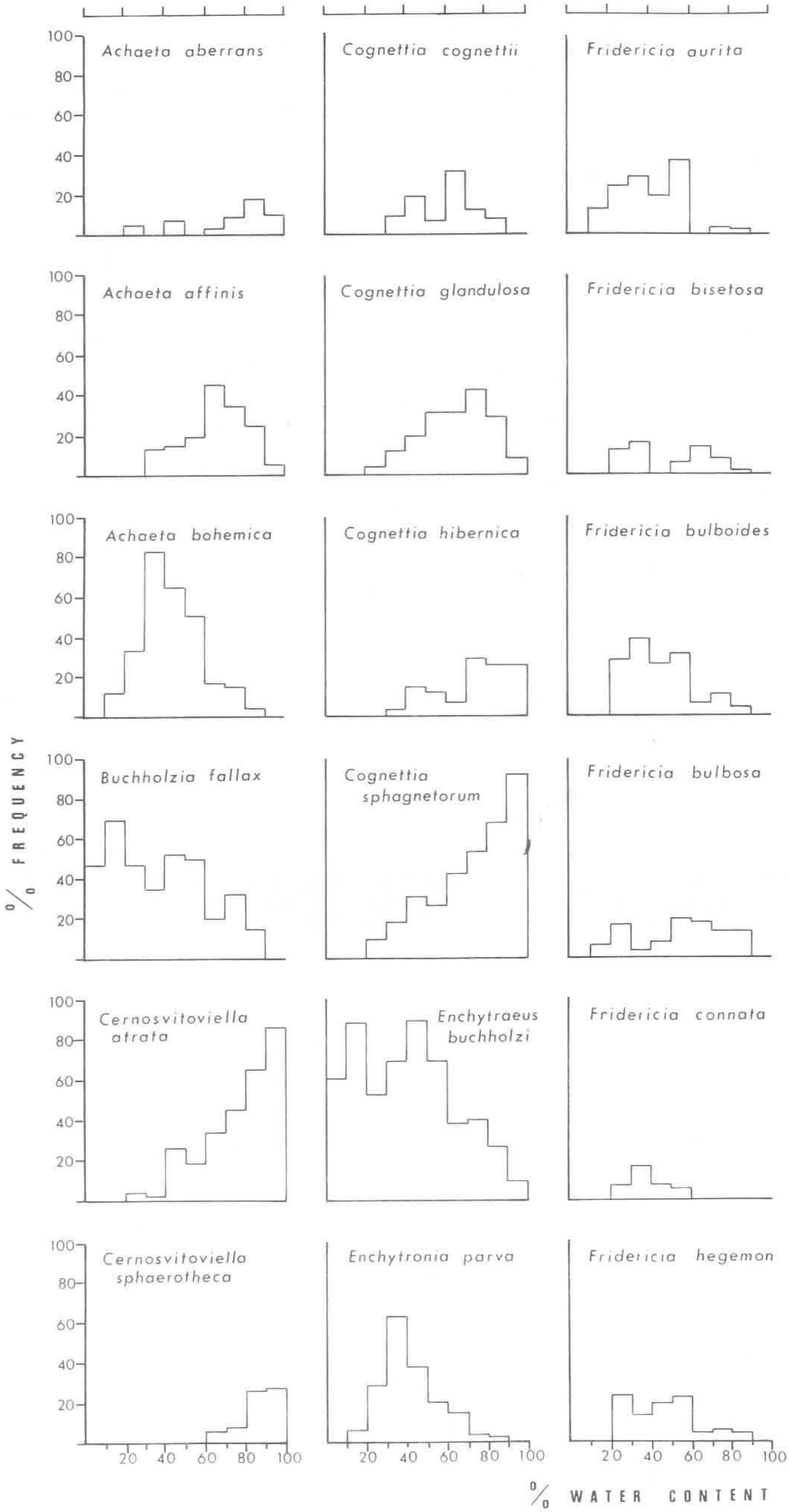
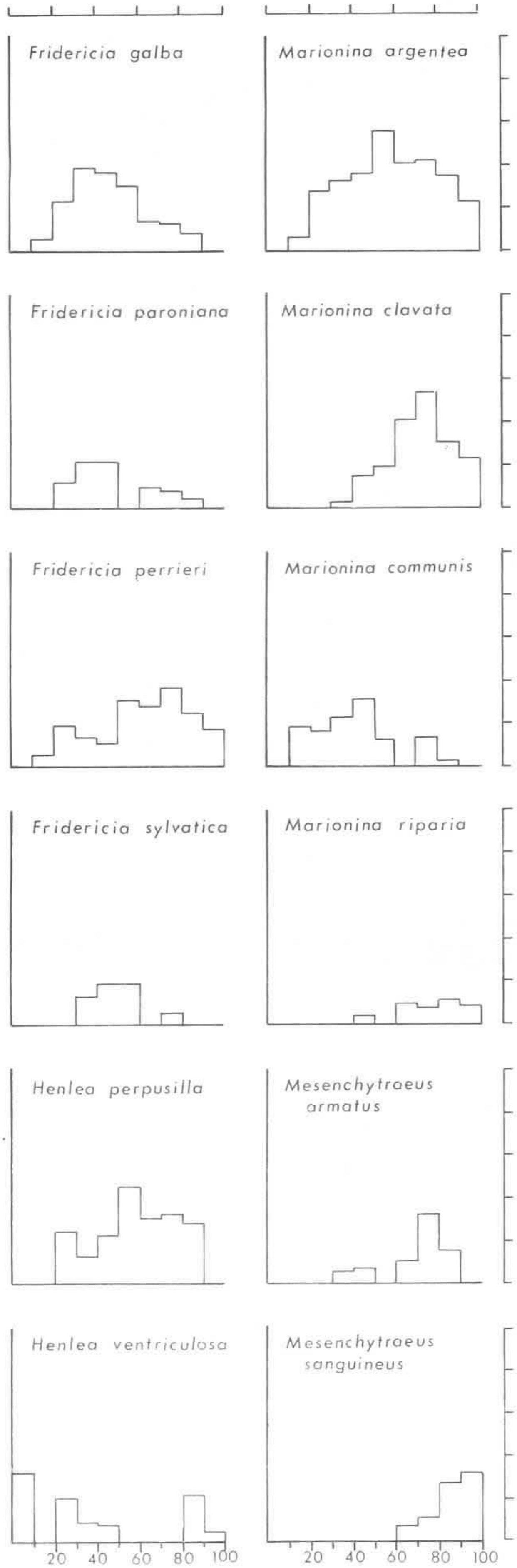


Fig. 4. Percentage frequency of 30 species in relation to soil water content.


Fridericia galba
Marionina argentea
Fridericia paroniana
Marionina clavata
Fridericia perrieri
Marionina communis
Fridericia sylvatica
Marionina riparia
Henlea perpusilla
Mesenchytraeus armatus
Henlea ventriculosa
Mesenchytraeus sanguineus
20 40 60 80 100
20 40 60 80 100

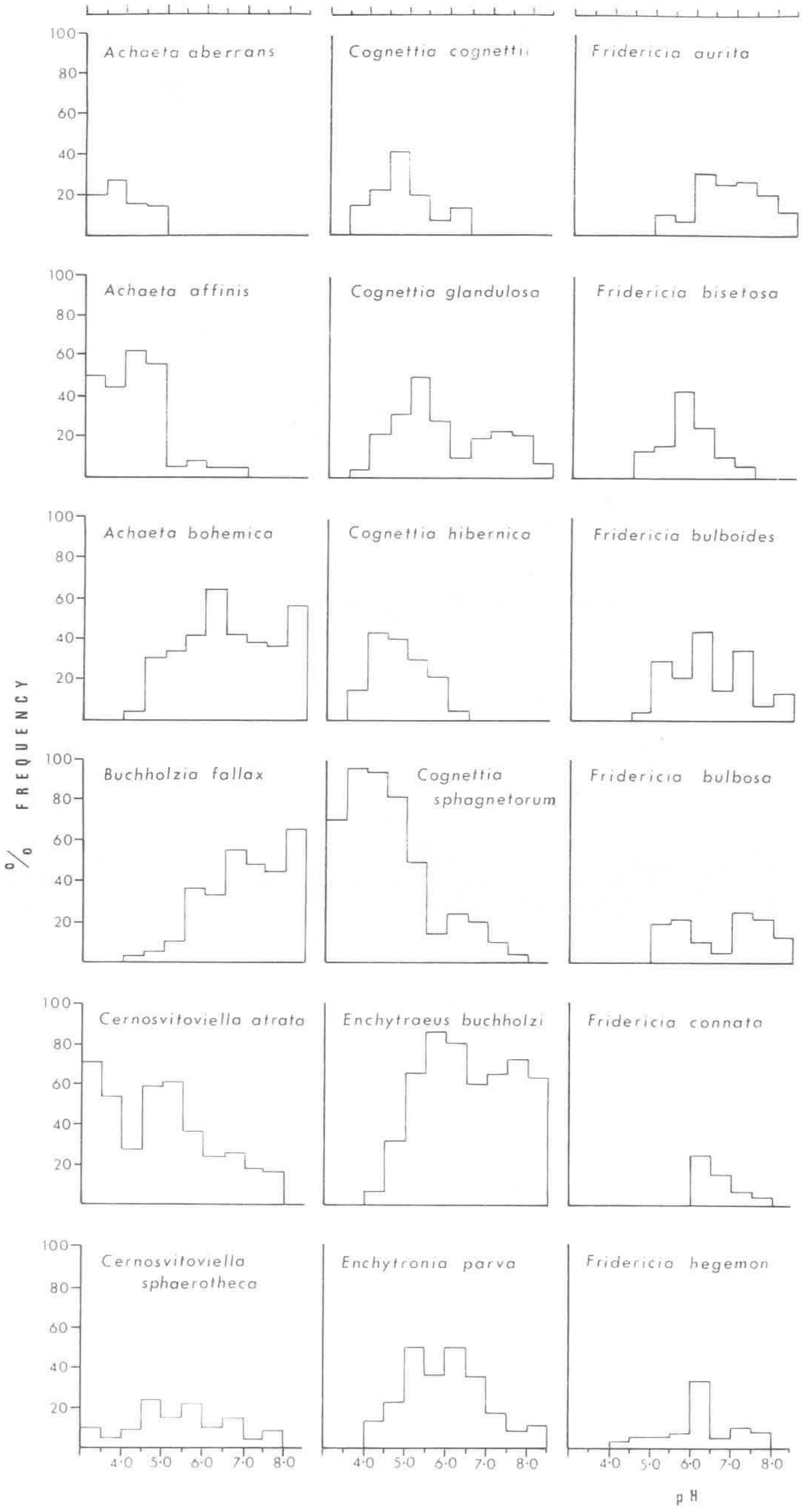
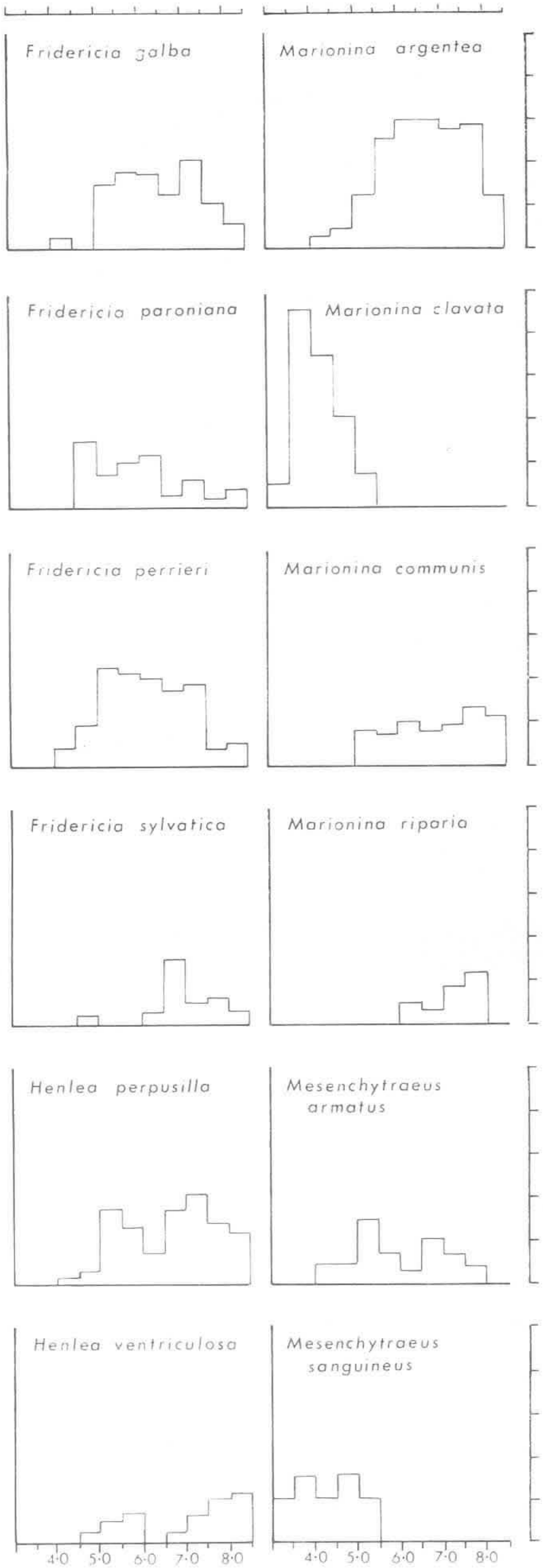


Fig. 5. Percentage frequency of 30 species in relation to soil pH.



Fridericia galba
Marionina argentea
Fridericia paroniana
Marionina clavata
Fridericia perrieri
Marionina communis
Fridericia sylvatica
Marionina riparia
Henlea perpusilla
Mesenchytraeus armatus
Henlea ventriculosa
Mesenchytraeus sanguineus
4·0 5·0 6·0 7·0 8·0
4·0 5·0 6·0 7·0 8·0

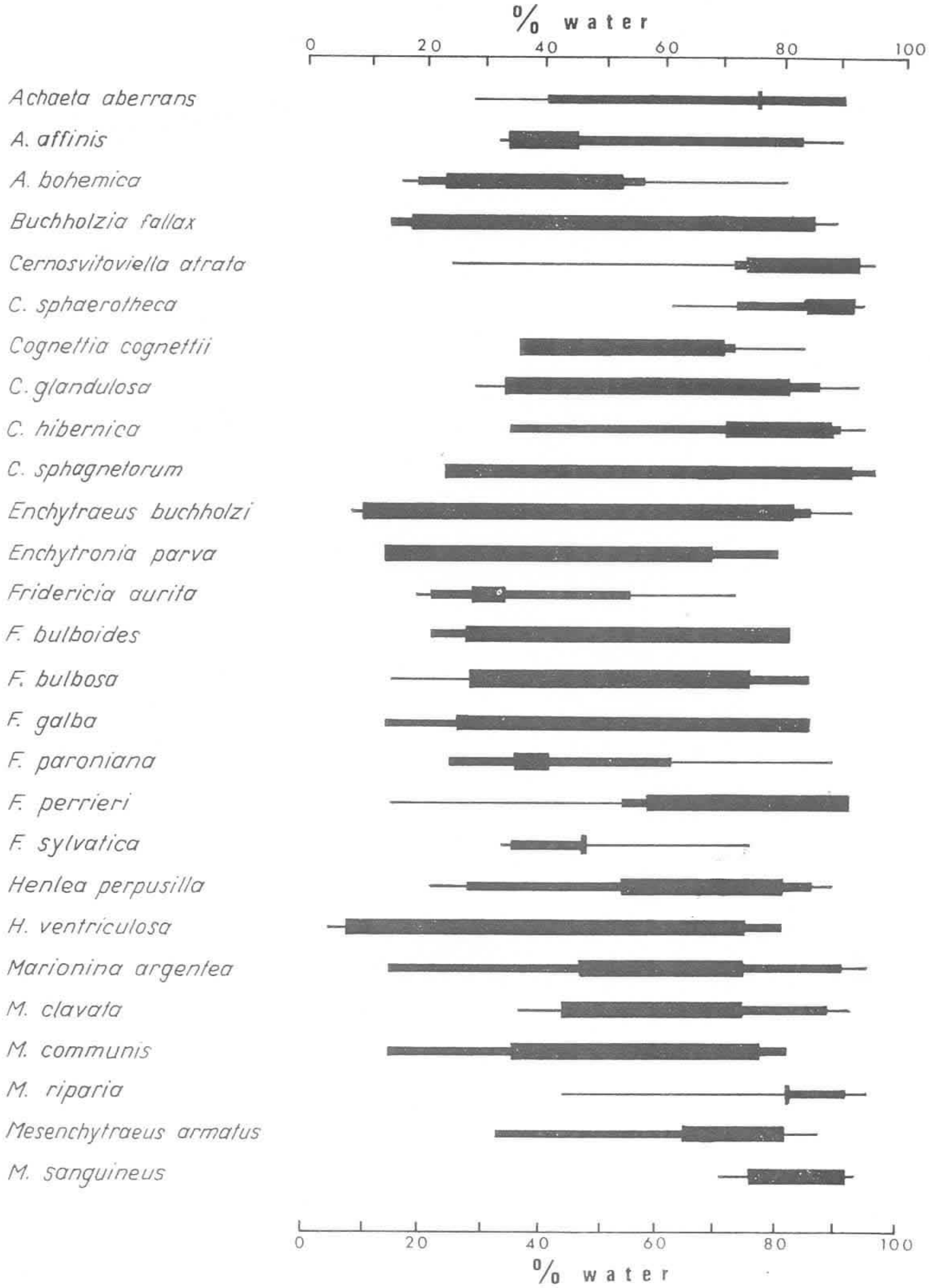


Fig. 6. Species density in relation to soil water content. (For explanation, see text).

3.3. Frequency of occurrence in relation to *p*H

From Fig. 5 it is seen that no species occurs throughout the entire *p*H range and that all species show preference for a part of the *p*H spectrum. A critical point on the scale is around 5.5 According to *p*H preferences, species may be classified as follows:

(1) Acidophils

(a) always in *p*H < 5.5: *Achaeta aberrans*, *Mesenchytraeus sanguineus*, *Marionina clavata*.

(b) more frequent in *p*H < 5.5: *Cognettia sphagnetorum*, *C. cognettii*, *C. hibernica*, *Achaeta affinis*

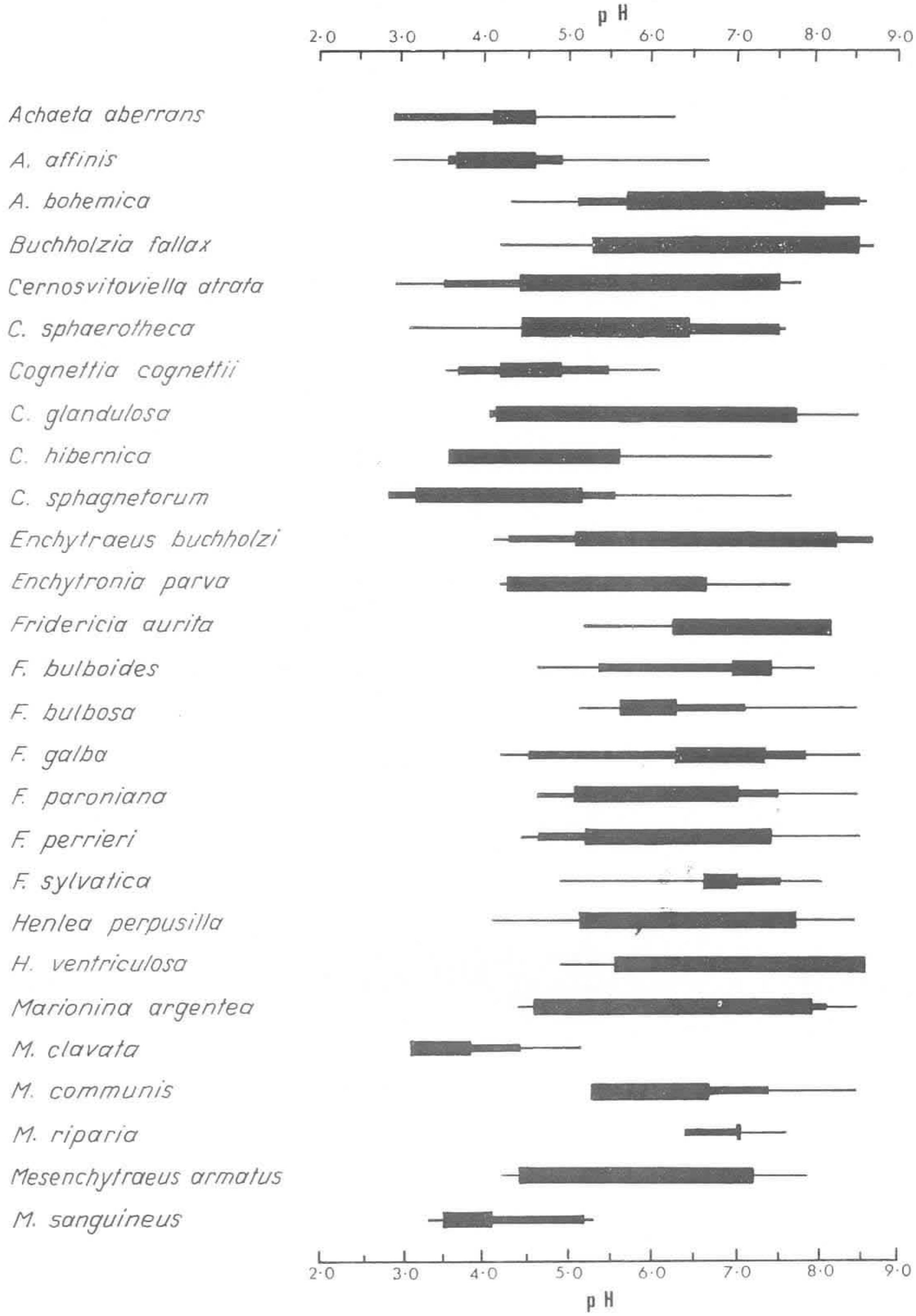


Fig. 7. Species density in relation to soil *p*H (For explanation, see text).

(2) Neutro-basophils
- (a) always in *p*H > 5.0: *Fridericia aurita*, *F. bulbosa*, *Marionina communis*.
- (b) always in *p*H > 6.0: *Fridericia connata*, *Marionina riparia*.

(3) Wide ranging species. All, however, show preference for a certain part of the scale.

*p*H is, of course, a reflection of the base-status of a soil and, especially of the level of calcium ions. An ordination of *p*H and exchangeable calcium for all samples (not shown) indicates a definite relationship but there is sufficient scatter to allow the two factors to be considered separately. Frequency distributions for the same species in relation to calcium show the same trends as for *p*H but some are polymodal and the relationship is less clear. A critical point on the calcium scale is at around 3,000 ppm which more or less separates calcicoles from calcifuges.

3.4. Species density

So far the ecological preferences of the species have been evaluated by reference to presence or absence only without consideration of numbers. It may be assumed that a species only occurs in high density within a limited part of its total range and that in situations close to its limits of tolerance, where its competitive powers are weak, it may be present only as an accidental species represented by few individuals. For animals such as enchytraeids which have a tendency to aggregate, it also seems reasonable to suppose that the aggregations will form where conditions are appropriate, even if the reasons for clustering are not directly related to environmental factors. Knowledge of the conditions under which a species may exist in high density can thus be useful in assessing ecological suitability of a habitat.

In sections 3.5 – 3.7, high density populations (or aggregates) are recognised as those in which the number of individuals per sample is greater than the mean + 1 SD for that species (Table 1) — represented by wide bars in Figures 6 and 7. Moderately high densities are those in which the number is greater than the mean but less than 1 SD — bars of medium width. Narrow bars indicate the range over which the species only occurs in dentities less than the mean. Note that a wide bar shows that a species can occur in high densities although it may not always do so. *Fridericia bisetosa*, *F. hegemon* and *F. connata* have been omitted due to insufficient data.

3.5. Species density in relation to water content (Figure 6)

Most species occur in high density within a limited part of their moisture range. When Figure 6 is compared with the frequency histograms (Figure 4) it is seen that for most species, frequency modes fall within the range of high density samples. Six species form high densities at or near the upper limit of their range *(C. atrata, C. sphaerotheca, M. sanguineus, F. bulboides, F. galba, F. perrieri)*; six species form high density at or near the lower limit of their range *(A. affinis, C. sphagnetorum, C. cognettii, E. buchholzi, E. parva, H. ventriculosa)*. These results suggest that high water content is the important limiting factor for some species while low moisture is more important for others. *E. buchholzi* and *H. ventriculosa* are the only species which can reach high density at less than 10% water, but five species can do so at more than 90% *(C. atrata, C. sphaerotheca, F. sphagnetorum, M. sanguineus, F. perrieri)*. In general, therefore, more species are adapted to very wet than to dry soils.

3.6. Species density in relation to *p*H (Figure 7)

The range of high density populations is even narrower than for water content and in the majority of cases this range corresponds to a frequency mode in Figure 5 or is not far removed from it. Three species form high densities at or near their upper limits and may thus be limited by acidity *(B. fallax, H. ventriculosa, F. aurita)*. Six species form high densities at or near their lower limits and may be limited by high *p*H *(C. glandulosa, M. armatus, M. sanguineus, E. parva, M. clavata, M. communis)*. Only two species occur in high density at *p*H less than 3.5 *(C. sphagnetorum* and *M. clavata)* but five species can do so at a *p*H greater than 8.0 *(A. bohemica, B. fallax, E. buchholzi, F. aurita, H. ventriculosa)*. Thus more species are adapted to alkaline than to very acid conditions.

3.7. Effects of other chemical parameters

The effects of other chemical factors are not generally apparent by the methods used here. Frequency distributions tend to be polymodal and there is little correlation between density and concentrations of the substances measured. More species are absent from soils with very low levels of organic matter, nitrogen, C/N, and phosphorus than from those with high levels and more species are absent from soils with high levels of potassium, magnesium and sodium than from those with low levels. There is a tendency for species to form high densities at relatively low levels of nitrogen, phosphorus, potassium, magnesium and sodium

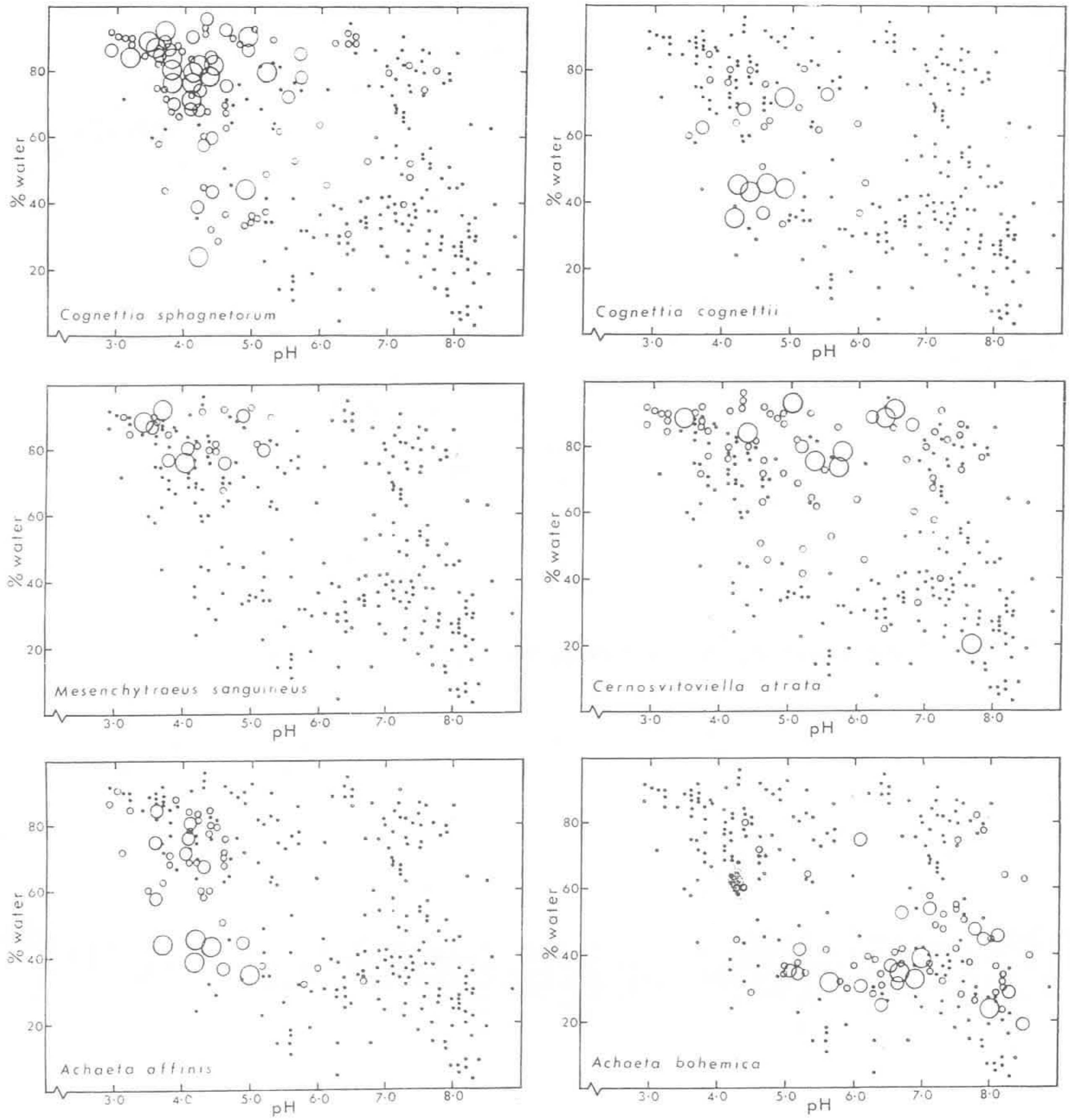


Fig. 8. The occurrence of enchytraeid species in relation to *p*H and water content (for explanation see text).

and for numbers to be reduced at high levels, particularly in the case of phosphorus. Only in relation to organic matter do more species form high density populations near the upper limit of their range than at the lower limits. Organic matter is probably an important factor limiting the number of enchytraeids.

3.8. Relative importance of *p*H and water

As a means of determining the relative importance of *p*H and water as ecological determinants, samples in which the species occurs have been plotted on a *p*H/water ordination using three sizes of symbols to represent density (Figures 8 and 9). The symbols correspond to high density, moderately high density and low density as for the three bar thicknesses in Figures 6 and 7 (explained under 3.4). Values less than the mean-1SD are rare because frequency distributions for enchytraeid abundance are almost always positively skewed (Nielsen 1954; O'Connor 1957). Samples in which the species does not occur are also shown. The distributions of 12 species are presented in this way.

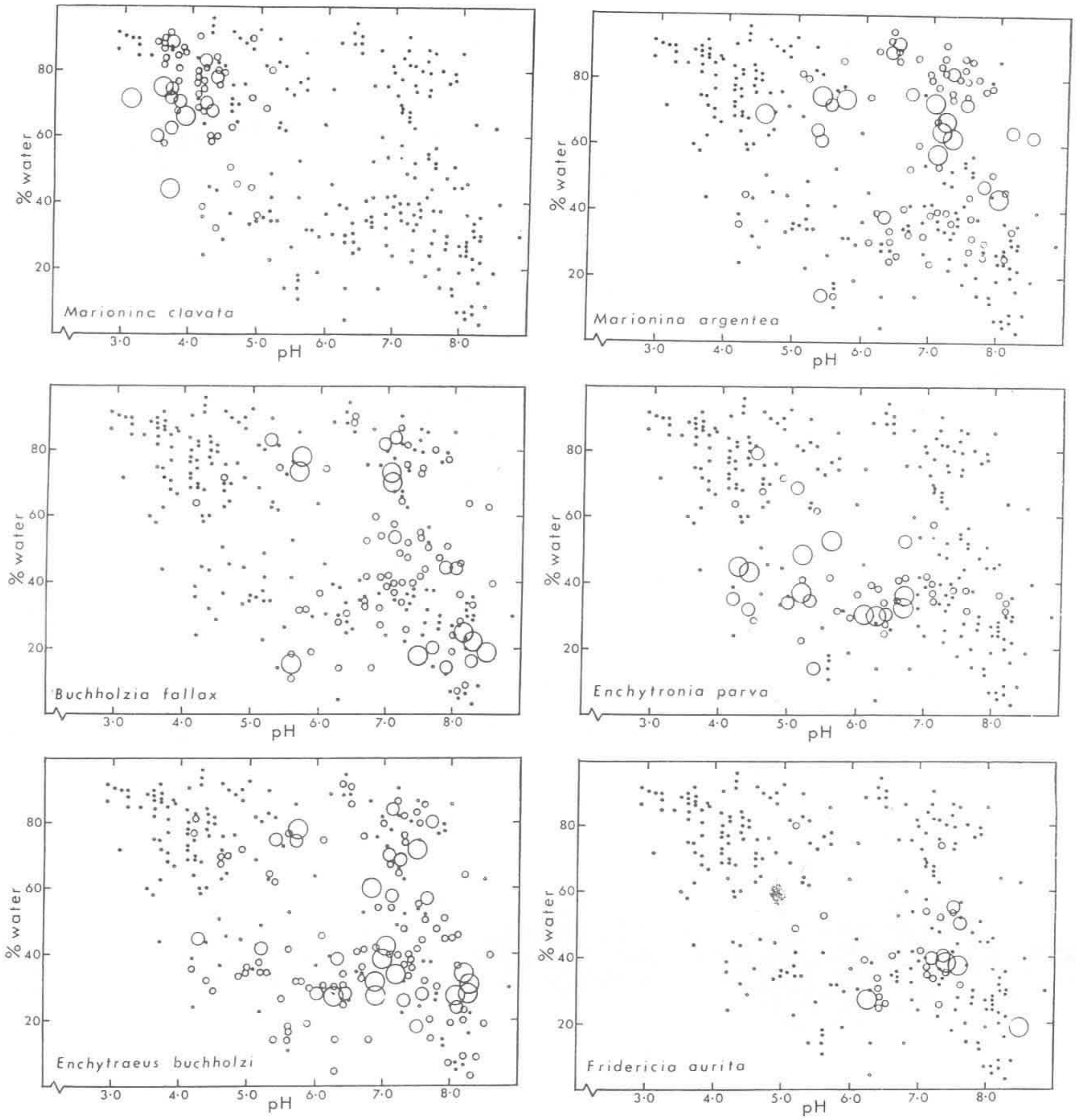


Fig. 9. The occurrence of enchytraeid species in relation to pH and water content (for explanation, see text).

If a line is drawn around high density samples, the shape of the area enclosed indicates the relative importance of pH and water content for the species. A shape which is elongated vertically, e.g. *Achaeta affinis*, *Cognettia sphagnetorum*, *Marionina clavata* shows that the species is limited principally by pH while a shape elongated horizontally, e.g. *Achaeta bohemica*, *Cernosvitoviella atrata*, *Marionina argentea*, *Enchytronia parva* indicates that the species is primarily water limited. Where the shape is not elongated, neither pH nor water are dominant factors. In the case of *Buchholzia fallax*, two centres of distribution are apparent. The samples with low water content are nearly all from sand dunes where specimens show morphological differences and may be genetically distinct. It is suggested that scatter diagrams of the type used here may be useful in resolving taxonomic difficulties, providing a sufficient number of samples is used.

4. Discussion

Both frequency of occurrence and high density have limitations as indications of ecological suitability. For example, high frequency does not necessarily indicate ideal conditions. A species may occur frequently in low numbers near the limit of its ecological range if the habitat is one in which extremes are rare. *Marionina argentea* occurs frequently in woodland leaf litter (50% of samples) but always in low density. This species is dependent on adequate moisture levels and although the water content of leaf litter is not particularly high, very low levels are usually rare. The relatively high frequency of *M. argentea* in the 20–50% water content range (Fig. 4) may thus be misleading. The use of population density as an indication of habitat suitability can also be unreliable. It is generally accepted that when an organism occurs in high density its ecological requirements are at an optimum. The converse, however, is not necessarily true, i.e. when an organism is rare or absent, one cannot conclude that conditions are unsuitable. Historical factors such as exceptional climatic conditions in the recent past, disease, unusually high numbers of predators and so on may have caused a temporary drop in numbers. For this reason, low densities of a species within its high density range have been ignored in this study. Generally speaking, the limits of tolerance of a species are shown by its distribution and its preferred or optimum levels by numbers, population density being a good indication of an animal's ability to compete. However, the spatial and temporal variation in numbers which characterise enchytraeid populations made it difficult to obtain reliable information on densities without a great deal of effort. The results presented in 3.5—3.7 can only be used as indications of general trends.

The poor correlation between enchytraeid distributions and plant associations which has been demonstrated does not agree with the findings of other authors. ABRAHAMSEN (1972) found that characteristic assemblages of enchytraeids corresponded quite closely with plant associations in Norwegian coniferous forests. In a more extensive survey of Fennoscandia and Spitzbergen, NURMINEN (1967) also found that characteristic groups of species were present in the different vegetation types although the latter were not really comparable with those in Ireland. In the English Pennines where moorland sites are very similar to equivalent habitats in Ireland, differences in enchytraeid species lists could be linked to a series of plant associations representing bog, heath and limestone grassland (SPRINGETT 1970). In this sequence, differences are easily explained by differences in soil acidity. SPRINGETT also found that 3 out of 20 species were confined to soils with a high proportion of peat and that species of *Fridericia* and *Achaeta* were absent from peat. In Ireland, both genera occur frequently in peat and mor humus.

The only study of natural populations of enchytraeids in which chemical and physical properties of soil were examined is that of ABRAHAMSEN (1972) who records values of *p*H, loss on ignition, nitrogen, calcium, potassium, manganese, magnesium, sodium and base saturation for a range of Norwegian forest soils. Although he found significant differences in total density and species diversity with increase in *p*H and calcium, he was unable to discover a direct relationship between enchytraeid fauna and the chemical properties of the soils by analysis of individual sample units. The soils studied, however, did not cover the wide range of conditions included in this survey and so limits of tolerance may not have been apparent.

The lack of clear correlation between enchytraeid distribution or abundance and most chemical factors in this study has several possible explanations. (1) Sampling was not as efficient as for water, *p*H or organic matter. (2) Comparisons between frequency distributions suggest that the effect of one factor can mask or distort that of another so that if there is a severe deficiency of one substance, deficiencies which are less severe may be difficult to detect. (3) It is possible that the wrong things have been measured. There is very little information on the nutrient requirements of invertebrates and practically none on the chemical forms in which essential elements can be absorbed. Exchangeable forms are the easiest to measure but may not be the only forms available to enchytraeids. (4) Finally, it is possible that while enchytraeids may be limited by severe deficiency or excess, intermediate levels are irrelevant, i.e. there is no continuously varying effect and no narrow optimum.

The results presented seem to show that both distribution and abundance of enchytraeids are closely related to water content and *p*H although it cannot be assumed that these factors are acting directly to influence individuals. *p*H especially reflects a variety of soil properties and may influence a whole series of other organisms including predators and foot items such as microflora. It is, however, an easy parameter to measure. Water content is probably even more important than the results suggest. Wetness, as experienced by a soil organism, is notoriously difficult to define. Moisture levels can fluctuate widely throughout the year and the use of weight as a means of estimating water content introduces errors resulting from differences in the specific gravity of solids (e.g. leaf litter v. sand).

Estimation of pF, usually considered to be a more meaningful measurement of soil moisture, it not applicable to the supersaturated soils so frequent among the chosen sites. The fact that single measurements of wet weight have proved useful is itself an indication of the importance of water as a factor controlling enchytraeid distribution.

Although water content and *p*H are probably limiting at both ends of a species range of tolerance, high densities often occur near one end. This suggests the influence of competitive pressures. In the case of species abundant in very acid soils, densities are among the highest recorded and it appears that these species take advantage of the absence of competition in habitats unfavourable to other enchytraeids and also to other decomposers such as earthworms as suggested by Abrahamsen (1973). Competitive exclusion may also explain the failure of enchytraeids as a whole and most of the individual species to form high density populations at high nutrient levels (especially N and P). Calculations of nitrogen budgets summarised by Satchell (1967, 1980) suggest intense competition for this element in which earthworms play an important part. In fertile soils, a few highly successful organisms such as earthworms, may play a dominant role in the nutrient economy while others, unable to compete effectively, are reduced in numbers. The limiting effect of high concentrations of salts such as sodium and magnesium, on the other hand, may be more direct, e.g. through their influence on the internal osmotic balance.

The Enchytraeidae as a whole show great ecological adaptability and some species are numerically very important in situations where many other groups are unable to survive, e.g. in acid mor and sewage beds. Nevertheless, the family is relatively homogeneous, both morphologically and biologically. All members live within substrates and have, broadly speaking, the same feeding habits and it might be supposed that the different species are competing for the same resources. However, the differences in food selection and vertical distribution demonstrated by other workers and the often striking differences in ecological ranges shown here indicate that the species have in fact achieved a considerable degree of niche separation.

5. Summary

A survey of Irish terrestrial enchytraeids is described in which the ecological distribution of the species is related to twelve parameters: vegetation, soil texture, water content, organic matter, total nitrogen, C/N, *p*H and exchangeable calcium, potassium, phosphorus, magnesium and sodium. The ecological limits and preferences of some common species are deduced from the results of quantitative sampling using two criteria: frequency of occurrence and the presence of high density populations.

Most species occurred in a wide range of vegetation types. The only textural characteristic of the soil which appears to be important is the proportion of humus. Among the parameters measured, water content and *p*H show the greatest influence on species distribution. The different species have characteristic, and often, quite different ranges in relation to these factors. The relative importance of water and *p*H varies with the species. High densities often occur at low *p*H and at low nutrient levels. It is suggested that many enchytraeid species are able to exploit the resources in poor soils and become non-competitive in more eutrophic conditions.

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